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THE  
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TEMPERATURE COEFFICIENTS IN PLANT GEOGRAPHY  
AND CLIMATOLOGY<sup>1</sup>

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(WITH THREE FIGURES)

**Introduction**

Plant geographers and climatologists have long been convinced that temperature is one of the most important of the conditions governing the distribution of plants and animals, but very little has as yet been accomplished toward finding out what sort of quantitative relations may exist between the nature of floral and faunal associations and the temperature conditions that are geographically concomitant therewith. The progress of descriptive ecology has shown clearly enough that these associations have their geographical limits, and increased accuracy of description has developed hand in hand with the idea that association boundaries must be considered as peripheries of certain complexes of environmental conditions. It is common, in recent papers upon plant and animal geography, to give considerable attention to descriptions of the climatic complexes which characterize the vegetational or faunal areas dealt with, but such description of climates has thus far usually consisted in the mere quotation or compilation of various meteorological data. In order to correlate these data with physiological phenomena, in such a way as to throw light upon the effective climatic

<sup>1</sup> Botanical contribution from the Johns Hopkins University, no. 36.

characteristics of the areas occupied by the respective associations, it will first be necessary to devise methods, and frequently instruments also, by which the climatic conditions of any given area may be so integrated as to bring out their relations to the processes of growth and reproduction in organisms. In the beginning, such methods will usually need to deal with single conditions or factors as they influence physiological phenomena, but biological science must eventually appreciate that single conditions, or any group of conditions comprising less than all the effective ones, cannot be considered as determining natural processes. Complexes of environmental factors must needs be analyzed into simpler ones, for purposes of study, but after knowledge of the effectiveness of each has been experimentally obtained (through maintaining all conditions other than the one in question not only constant but at a known and stated value or intensity), they must then be recombined and their effects integrated before real knowledge may be available.

If a plant thrives in a given locality, so as to form a part of the flora of that locality, it is obvious that there have not occurred here, since the arrival of its ancestors, any environmental conditions incompatible with its existence. In this we merely make the biological observation that the organism is and has been *adapted*<sup>2</sup> to the environment in which we find it, and that the environment is and has been *adapted* to the organism. Thus, when the range or geographical extent of an organism or association has been determined, it is clear that the area or areas so circumscribed have been characterized for some time in the immediate past by conditions none of which have been adverse enough to annihilate the forms dealt with. Outside of these areas the conditions have not been such as to bring about the permanently successful entrance of these forms, up to the present time. It is of course clear that entrance may have been accomplished here, but if this has been the case each such entrance must have been followed by the occurrence of annihilating conditions.

<sup>2</sup> On a somewhat matter-of-fact view of biological adaptation, see the following paper: LIVINGSTON, B. E., Adaptation in the living and non-living. *Amer. Nat.* 47:72-82. 1913. See also HENDERSON, L. J., The fitness of the environment. New York. 1913.

Furthermore, the internal conditions (or the nature) of an organism being duly considered, the success attained by it in any locality is an index of the extent to which the environmental conditions of that place have been favorable to successful growth, both vegetative and reproductive. Thus it frequently becomes apparent that the conditions of one locality have been more or less favorable to the success of a given form than have those of another locality.

The difficulty, however, which ecological science has not yet been able to surmount lies in the extreme complexity of the system of conditions which affect the success of organisms. The numerous component factors of an environmental complex fall into categories of *water, non-aqueous materials, heat, light, and mechanical conditions*. It is obvious that the limiting condition that has prevented the occurrence of a certain plant, for example, in a given area, may belong to any one of the foregoing categories; mechanical conditions may have failed to bring the seed hither, moisture conditions, or other conditions of material supply or removal, may have annihilated the plant after it was really introduced, or annihilation may have followed from adverse temperature or light conditions, etc.

The distributional problem is made still more complicated and difficult by the perfectly clear but seldom emphasized proposition, that each separate or component condition of an environmental complex is a variable in at least two dimensions, as it were; each such condition must always be considered with regard to its *intensity* and also with regard to its *duration*. To illustrate by means of a water factor, a desiccated soil may cause the death of a given seed, but this result would probably not be accomplished if the soil were dry for only a day or a month; the condition of dry substratum must be maintained for a certain minimum period if it is to be effective as a limiting condition. Some less well defined environmental factors have to be considered in regard to a third dimension which may vary, namely, *quality*. Light, for example, may reach chlorophyll tissue in seemingly sufficient intensity and during an apparently sufficient time period to produce a requisite amount of carbohydrate, but this may fail to happen because the radiant energy is of too short or too long wave-length. Here quality is as important as is either intensity or duration.

Finally, the difficulties of distributional, as of other physiological problems, are greatly aggravated by the fact that each organism is always in process of internal alteration, passing thus through various more or less well defined and conveniently separable phases of development. Thus, a certain quality, intensity, and duration of the light condition may be wholly without sensible effect upon an unsoaked seed, while the same dimensions of the same factor may be fatal to the same plant when in a more active developmental phase. In the study of external conditions it is thus useless to attempt to establish relations between these and organisms, unless adequate consideration is given to internal conditions or developmental phases of the latter. Quantitative ecology must not only try to find out to what environmental conditions its organisms are subjected, and to what degree and for how long these conditions are present, but it must also determine during what developmental phases of the organisms the conditions are effective. It is this consideration which makes it quite impossible to establish ecological relations without adequate knowledge of the physiological nature, at different developmental stages, of the forms dealt with.

Leaving temporarily out of account those mechanical conditions which may, in the past, have acted to transport plants from one geographical area to another, we are aware that the environmental conditions which control growth and reproduction, after the introduction of an organism into a given region, are nearly always naturally in a state of flux. Day and night changes and the march of the seasons, together with more markedly irregular fluctuations in wind, precipitation, evaporation, etc., all produce their effects upon both living things and non-living ones, but these effects are usually much more pronounced in the case of organisms than in that of inanimate objects. As has been previously emphasized by one of the writers,<sup>3</sup> an organism furnishes, at any instant, a summation of the effects of all the processes which have gone on in the body during its previous developmental history. One of our greatest difficulties, however, lies in the fact that we are totally unable to differentiate this integrated record, but we may nevertheless be

<sup>3</sup> LIVINGSTON, B. E., Climatic areas of the United States as related to plant growth. *Proc. Amer. Phil. Soc.* 52: 257-275. 1913.

sure that each of its component terms involves at least a quality, intensity, and duration of some environmental factor. It is thus seen that what is most needed for etiological studies of the geographic distribution of organisms, as well as for all other studies which deal with the conditioning or causation of life processes, is comparative measurements of these processes, or of groups of them, and corresponding measurements of the conditioning environmental factors. To accomplish such measurements and thus to institute the requisite comparisons is now practically impossible in most cases; methods need first to be devised and then to be applied, and the world does not yet offer satisfactory facilities for either. Measurements which can be carried out in present-day laboratories, while applicable in some cases, especially with forms not influenced by light, are quite inadequate even for making a rational beginning in the quantitative study of environments in general. In planning a campaign for this sort of study it is obvious that the effects produced by any environmental factor cannot be adequately studied unless that factor, as well as all the other effective ones, is under control by the experimenter. A laboratory where such experimentation as is here indicated may be carried out is now feasible, with recent advances made in the physical sciences and in physiology, and the scientific and practical importance of the results to be obtained, especially from the standpoint of agriculture and forestry, may perhaps soon warrant the provision of the needed facilities, somewhere in the world.<sup>4</sup> Until such facilities may have become available, it will be profitable, however, to prepare the way for them by carrying out such quantitative or semi-quantitative comparisons between vital activities and environmental conditions as are at present possible.

The present paper involves some of the results of an attempt to find a rational method for interpreting climatic temperature data for phytogeographic purposes. This sort of study is somewhat simplified, in the case of plants, by the fact that the temperature of

<sup>4</sup> This need was strongly emphasized over two decades ago by ABBE, who also quotes DECANDOLLE to the same effect. See ABBE, C., First report on the relations between climates and crops. U.S. Dept. Agric., Weather Bureau, Bull. 36. p. 23, 1905.

the plant body follows very closely upon that of the surroundings, and that soil temperature and air temperature are, roughly speaking, somewhat closely related. Furthermore, the heat condition of plants, as approximately measured by the temperature of the surrounding air, varies only in respect to intensity and duration; qualitative fluctuations are not met with here. Geographically, the present study deals with the area occupied by the United States.

### Direct temperature summation

The effectiveness of temperature conditions to promote plant growth in any locality has been measured by phenologists,<sup>5</sup> by means of the direct summation of the daily mean temperatures, such summation extending through the period of any particular phase of plant development which might be considered; for example, the period extending from the time of germination to that of flowering or of seed-maturation. In these temperature summations a certain minimum temperature is assumed as a starting-point, and the amount added to the summation for each day as the season advances is the number of degrees, above the assumed minimum, which represents the mean temperature for that day. The minimum has sometimes been 0° C., more often a somewhat higher temperature. In the employment of such temperature summations, each station of observation is characterized each year by its summation index, and after a period of years these indices may be averaged to give a measure of the temperature factor in general, for that particular place.

In a way somewhat similar to that followed by workers in phenology, MERRIAM<sup>6</sup> has obtained normal summation indices of temperature for a large number of stations in the United States, and has presented these in the form of a chart showing climatic zones, each characterized by its own range of temperature summa-

<sup>5</sup> In this connection see ABBE, *loc. cit.*

<sup>6</sup> MERRIAM, C. H., Laws of temperature control of the geographic distribution of animals and plants. *Nat. Geog. Mag.* 6:229-238. 1894. The same work was again reported, in still more abbreviated form, in part III of the following paper: MERRIAM, C. H., Life zones and crop zones of the United States. U.S. Dept. Agric., Div. Biol. Survey, Bull. 10. 1898.

tion indices. So far as we know, this is the first chart of its kind to be prepared upon the basis of temperature summation, and the temperature zones of this writer have come into rather general use among American phytogeographers.

A method of direct summation, similar to those employed by phenologists but dealing in a more refined way with the temperature conditions of plant environments, has been described by MACDOUGAL.<sup>7</sup> This author summed the temperatures above the freezing-point of water for the period occupied by certain developmental phases of certain plants; but, instead of adopting as the terms of the summation the daily means or the means of daily maxima and minima, his integration was performed, with a planimeter, upon automatically traced thermograph records. The resulting indices of environmental heat conditions are expressed by MACDOUGAL in terms of "hour-centigrade-degree" units. This method has never been employed in climatological or phytogeographical studies, so far as we are aware. It seems to be the simplest and most promising of all the direct summation methods, but of course requires reliable thermograph tracings. Each year or season is to be treated separately, and the resulting annual indices may be averaged for a period of years, to give a normal index.

### Temperature efficiencies

Although such temperature summations as those of the phenologists and of MERRIAM have seemed in many instances to furnish data consistent among themselves and constituting on an empirical basis an apparently reliable criterion for the measurement of the intensity and duration aspects of the temperature factor, yet it must be regarded as highly improbable that any fundamental and general principle regarding the influence of temperature on plant life may be derived from the relations thus brought out. It seemed to us that the apparent value of temperature summations must rest upon some basic principle of physiology not indicated in the summations themselves.

<sup>7</sup> MACDOUGAL, D.T., The temperature of the soil. Jour. N.Y. Bot. Garden 3:125-131. 1902.



Now, as far as temperature influence is concerned, the most fundamental generalization that physiology has yet been able to attain is that which may be termed the principle of temperature coefficients. This is primarily the application of the chemical principle of VAN'T HOFF and ARRHENIUS to vital phenomena. This principle states that, within limits, the velocity of most chemical reactions doubles or somewhat more than doubles for each rise in temperature of  $10^{\circ}\text{C}$ .<sup>8</sup> The principle fails to hold rigidly, even in the somewhat vague form in which it is stated, but it seems to express in an approximate way a fairly general truth in chemical phenomena.

A considerable literature has developed about the application of this chemical principle in physiology. CLAUSEN<sup>9</sup> determined the rate of evolution of carbon dioxide from seedlings and buds at several different temperatures and found that this rate somewhat more than doubled for each rise in temperature of  $10^{\circ}$ , up to an upper limit of about  $40^{\circ}\text{C}$ . COHEN<sup>10</sup> calculated from measurements of O. HERTWIG<sup>11</sup> that the time consumed by developing frog's eggs, for the completion of certain developmental phases, about doubled for each *fall* in temperature of  $10^{\circ}$ . Miss MATTHAEI<sup>12</sup> studied the influence of temperature on the evolution of carbon dioxide from leaves in darkness and also on the fixation of this gas by leaves in light, and showed that the VAN'T HOFF-ARRHENIUS principle holds also for these plant processes. A temperature coefficient of the same order of magnitude as is required by this principle was found, for a number of different physiological pro-

<sup>8</sup> For one clear statement of this principle see VAN'T HOFF, J. H., *Lectures on theoretical and physical chemistry*, translated by R. A. LEHFELDT. London. No date (author's preface dated 1898). Part I. pp. 227 f.

<sup>9</sup> CLAUSEN, H., *Beiträge zur Kenntnis der Athmung der Gewächse und des pflanzlichen Stoffwechsels*. Landw. Jahrb. 19:893-930. 1890.

<sup>10</sup> COHEN, E., *Lectures on physical chemistry for physicians and biologists*. Translated by MARTIN H. FISHER. New York. 1902.

<sup>11</sup> HERTWIG, O., *Über den Einfluss der Temperatur auf die Entwicklung von Rana fusca und Rana esculenta*. Arch. f. Mikroskop. Anat. und Entwicklungsgesch. 51:319-381. 1898.

<sup>12</sup> MATTHAEI, GABRIELLE L. C., *Experimental researches on vegetable assimilation and respiration*. III. On the effect of temperature on carbon dioxide assimilation. Phil. Trans. Roy. Soc. London B 197:47-105. 1904.

cesses in animals, by LOEB<sup>13</sup> and his co-workers, and SNYDER<sup>14</sup> has emphasized the value of non-chemical temperature coefficients in the study of physiological velocities. An excellent statement of this whole problem, especially with regard to plants, is included in BLACKMAN's Dublin presidential address,<sup>15</sup> where he discusses also the determination of the effect of temperature on the rate of division of the flagellate *Chilomonas paramecium*, as carried out by MALTAUX and MASSART,<sup>16</sup> and points out that the temperature coefficient here really dealt with has a magnitude of about 2.4. BLACKMAN's concluding sentences in this address are worthy of quotation here, for their general bearing on the nature of the question with which we are dealing:

To me it seems impossible to avoid regarding the fundamental processes of anabolism, katabolism, and growth as slow chemical reactions catalytically accelerated by protoplasm and inevitably accelerated by temperature. This soon follows if we once admit that the atoms and molecules concerned possess the same essential properties during their brief sojourn in the living nexus as they do before and after.

In much of the work that has been published on vital temperature coefficients, relatively simple physiological processes have been considered, and it seems allowable to conclude, at least tentatively, that most of the elementary chemical processes of living things go on according to the principle of VAN'T HOFF and

<sup>13</sup> An apparently complete list of citations for the contributions bearing upon this general subject, including those here referred to, up to November 1908, is given in the following personally polemical article: LOEB, J., ROBERTSON, T. B., MAXWELL, S. S., and BURNETT, T. C., On the encouragement of Mr. CHARLES D. SNYDER. *Science* N.S. 28:645-648. 1908. This paper is to be read in connection with SNYDER's calmer reply: SNYDER, C. D., A reply to the communication of Messrs. LOEB, MAXWELL, BURNETT, and ROBERTSON. *Science* N.S. 28:795-797. 1908.

<sup>14</sup> SNYDER, C. D., Der Temperaturkoeffizient der Geschwindigkeit der Nervenleitung. *Arch. Anat. und Physiol., Physiol. Abt. Jahrg.* 1907. 113-145.

———, A comparative study of the temperature coefficients of the velocities of various physiological activities. *Amer. Jour. Physiol.* 22:209-334. 1908.

<sup>15</sup> BLACKMAN, F. F., The metabolism of the plant considered as a catalytic reaction. Presidential Address, Botanical Section, British Association, Dublin meeting, 1908. *Science* N.S. 28:628-636. 1908.

<sup>16</sup> MALTAUX, MARIA, and MASSART, JEAN, Sur les excitans de la division cellulaire. *Ann. Soc. Roy. Sci. Méd. et Nat. Bruxelles* 15:1-53. 1906; *Recueil de l'Inst. Bot. Bruxelles* 4:369-421. 1906.

ARRHENIUS, and that such processes possess temperature coefficients, within the ordinary limits of environmental temperatures, of an order of magnitude of from about 2.0 to about 2.5. This may be regarded as a fundamental principle in physiology.

When, however, many of these elementary or component processes are combined into a complex resultant, such as we have in physiological growth, for example, it is not immediately clear on a priori grounds that temperature coefficients of this same order of magnitude must obtain. RUSSELL<sup>17</sup> states rather authoritatively that "the effect of temperature on the *rate of growth* of a plant is in nowise like its effect in accelerating chemical change," and cites the work of BIALOBLOCKI<sup>18</sup> in support of this view. The last named writer studied the influence of temperature upon the rate of growth of barley, and his results appear to show (see RUSSELL's graph, p. 21) that the value of the temperature coefficient in this case alters markedly with the temperature itself. Considering, however, the fact that these results of BIALOBLOCKI appear to differ very markedly from those of the later workers who have dealt with the question, we are inclined not to give them such conclusive weight as does RUSSELL. In considering the matter before us, it is to be remembered that the principle of VAN'T HOFF and ARRHENIUS has never been supposed to hold, even for simple chemical reactions, excepting *between certain limits*, and that these limits should not be expected to be the same for all processes. Furthermore, as has been emphasized by BLACKMAN,<sup>19</sup> RUSSELL (*loc. cit.* pp. 20 f.), MITSCHERLICH,<sup>20</sup> and others, the full possible effect of a rise in temperature is frequently precluded by the failure of some other environmental condition correspondingly to alter. To illustrate, we may suppose (as BLACKMAN, *loc. cit.* 1908, suggests) that the

<sup>17</sup> RUSSELL, E. J., Soil conditions and plant growth. London. 1912.

<sup>18</sup> BIALOBLOCKI, J., Über den Einfluss der Boden wärme auf die Entwicklung einiger Culturpflanzen. Landw. Versuchsstat. 13:424-472. 1870.

<sup>19</sup> *Loc. cit.*; also BLACKMAN, F. F., Optima and limiting factors. Ann. Bot. 19:283-295. 1905.

<sup>20</sup> MITSCHERLICH, E. A., Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenenertrages. Landw. Jahrb. 38:537-552. 1909.

———, Über das Gesetz des Minimums und die sich aus diesem ergebenden Schlussfolgerungen. Landw. Versuchsstat. 75:231-263. 1911.

velocity of a given chemical process doubles with each rise of  $10^{\circ}$  in temperature, but that the process is retarded by the accumulation of the products of the reaction. In such a case it is obvious that, with increasing temperature, a point might sooner or later be reached at which the removal of these products might not proceed rapidly enough to allow the full temperature effect to become manifest. Thus, the rate of removal of the products must be adequately increased with the rise in temperature; otherwise the effect of this rise becomes masked by the effect of another variable, namely the mass action of the products. From these considerations it does not seem surprising that complex vital processes such as growth may frequently fail, under natural conditions, to exhibit the usual chemical temperature coefficient. In some of these cases, proper alterations in other environmental factors might disclose the otherwise obscured coefficient; in other cases the limitations might lie in the nature of the protoplasmic mixture, and the obscuring of the coefficient might persist in spite of any attempt at external adjustment.

The most satisfactory study on the influence of temperature upon growth rates in plants, so far as our knowledge goes, is that of PRICE,<sup>21</sup> who determined temperature coefficients for the opening of flower buds of the plum, peach, apple, and other fruits, and found the VAN'T HOFF-ARRHENIUS principle generally to hold. Beginning with resting buds, the time period required for blooming is reduced about one-half for each rise in temperature of  $10^{\circ}$  C. The same author figures maize seedlings which suggest that the rate of growth in length of shoot about doubles for each rise of  $10^{\circ}$ .

The present aspect of the entire question leads us to the conclusion that there are many cases in which growth rates and other complex processes in plants and animals exhibit temperature coefficients of about 2.0, and that, in other cases, this same coefficient may probably be operative, but may be obscured by the limiting effect of some other environmental or internal condition. It must also be supposed that temperature coefficients of other orders of magnitude may be encountered, not only for complex life

<sup>21</sup> PRICE, H. L., The application of meteorological data in the study of physiological constants. Ann. Rep. Virginia Agric. Exp. Sta. 1909-1910.

processes, but also for some of the elementary ones. The elementary processes of growth itself (that is, the *immediate* phenomena which condition growth, the ones first met with in a rational attempt to analyze the complex process) are all or nearly all physical in nature, and not to be regarded as chemical. They include such physical changes as coagulation, precipitation, alterations in elasticity, swelling by imbibition and osmotic action, and many others. It thus becomes apparent that the reason why the chemical temperature coefficient appears to be manifest in growth phenomena cannot be that these phenomena are primarily and immediately chemical in their nature, but that, physical though they are, they depend in turn upon other internal changes that are unquestionably chemical. Thus, for a single example, the precipitation or coagulation of colloid material met with in the formation of cell walls in plants must logically be dependent upon the continuous presence of the precipitating substances in the peripheral layer of the protoplasm of each growing cell, and within a certain range of concentration, and this continuous presence indicates chemical processes which must be effective not very far back (in the chain of causally connected phenomena) from the precipitation itself. Under such circumstances it might be expected that a physical complex such as growth would frequently exhibit a chemical temperature coefficient.

The fundamental physical changes which make up growth have not yet been studied sufficiently to permit the making of any estimate regarding the orders of magnitude of their temperature coefficients; nevertheless, we are certain that some of these coefficients possess values widely different from that postulated by the VAN'T HOFF-ARRHENIUS principle. Thus, for example, the temperature coefficient of osmotic pressure, within the range encountered in living cells, approximates the familiar quantity 0.003665, as usually employed, for each single degree above the zero point of the Centigrade scale, the pressure at 0° being taken as a basis. If the pressure at 0° be considered as unity, the pressures at 4°, 14°, 24°, and 34° become 1.01466, 1.05131, 1.08796, and 1.12461, respectively, and for each 10° rise in temperature the pressure is increased by only about 0.04.

On the other hand, within the temperature range with which physiology deals, some physical phenomena exhibit temperature coefficients somewhat closely approximating the order of magnitude called for by many chemical reactions. To illustrate, the vapor tension of water at  $4^{\circ}$  is 6.097 mm. of mercury, and the tensions at  $14^{\circ}$ ,  $24^{\circ}$ , and  $34^{\circ}$  are 11.908 mm., 22.184 mm., and 39.565 mm., respectively. Here the three temperature coefficients corresponding to these three rises of  $10^{\circ}$  in temperature are 1.95, 1.86, and 1.78, respectively. The vapor tension of water must be accounted an important condition for all transpiring plants; this pressure may be regarded as the driving force of evaporation, thus constituting the fundamental energy condition of the phenomenon of transpiration.

#### **Application of temperature coefficients to climatology**

If the processes of growth and development do really exhibit temperature coefficients, it is plain that the study of environmental integrations should deal with these rather than with temperatures directly. It is also plain that if direct temperature summations do, in certain cases, furnish adequate criteria for evaluating the effectiveness of temperature conditions, then this state of affairs must be true only within certain limits, and the experimental study of temperature coefficients furnishes the only adequate means for locating these limits and establishing the direct summations upon a rational basis. It seems worth while, therefore, to make a first attempt in the direction of the application of velocity coefficients to the study of effective temperature conditions as these characterize climatic and vegetational areas. Such an attempt, of course, must be very unsatisfactory from an idealistic point of view; nevertheless, it should serve to emphasize the need of quantitative studies in this connection and should also be of value in showing what sort of climatic and distributional observations are most likely to be of value as ecology becomes more exact.

For the present study we have tentatively assumed that the temperature coefficient of growth and development has a value of 2.0 for each rise of  $10^{\circ}$  C., a value which somewhat closely approxi-

<sup>22</sup> BIEDERMAN, R., *Chemicker Kalendar*. 1903. Bd. 2. Berlin. 1903. pp. 84, 85.

mates those which have so far resulted from most physiological studies of temperature relations. It seems that this value is more likely to be too low than too high for ranges of temperature commonly met with in nature, but the present status of the problem does not warrant any attempt at a closer approximation. Indeed, it seems almost certain that the magnitude of the temperature coefficient will be found to vary, not only with different plant forms and with different stages of development of the same form, but also with the values of the temperatures considered. It is readily conceivable that the relation which we are seeking may be determined satisfactorily only by the use of a temperature coefficient which is itself a variable, changing in value with the progress of the organism through its life cycle and with the annual march of the seasons, as well as with variations in the temperature itself. The time is not yet ripe, however, for even an *a priori* discussion of this matter.

Having tentatively established the temperature coefficient which is to be taken as a measure of the effectiveness of temperature in advancing growth (the intensity factor), we must make a similar assumption in case of the duration factor. For what period of time should we apply our assumed temperature coefficient? This question is precisely the same as the one met with in connection with direct temperature summations, and its answer, as in that case, must involve the relation of time to the developmental stages in the organisms concerned. Since it is here desired to deal with the whole matter in the broadest and most general way, it is requisite to fix upon a time period, which will, as nearly as possible, approximate the period of active growth in the majority of higher plants. As one of the authors<sup>23</sup> has emphasized, the controlling climatic conditions are primarily effective for most plants only during the season of active growth. This growing season may be approximated, for phytogeographical purposes, as the average or normal length of the frostless season, the number of days which intervene between the average date of the last killing frost in spring and the first in autumn. This has been adopted as the time factor in the present study.

<sup>23</sup> Proc. Amer. Phil. Soc. 1913; as already cited.

Since the individual data from which was derived DAY's chart<sup>24</sup> of the average length of the frostless season in the United States have not been published as such, the average lengths of the frostless season for the various stations in the United States with which we have been concerned have been taken from the 106 climatic summaries by sections,<sup>25</sup> published by the Weather Bureau.

Not only is it necessary to fix upon the length of time during which temperature integration is to be made, it is also requisite, for each station, to establish the month and day with which the summation is to begin, and likewise that with which it is to terminate. These dates must of course be chosen with reference to the beginning and ending of the period of active growth. The first is here taken as the date *next following* the average date of the last frost in spring, and the second as the average date of the first frost in autumn. If the dates for the beginning and end of the assumed growth period were determined from daily mean temperatures (as in case this period were taken as beginning with the first day in the year having a daily mean of 40° F. or above, and ending with the last day having this temperature), then they should bear a definite relation to the real first and last dates of the active period. Such methods have been frequently used in phenology. By our method, the beginning and end of the average period of active growth are determined from frost data rather than from mean daily temperatures. The two methods would probably prove equally satisfactory, with no great discrepancy in most cases.

The geographical distribution of plant associations and of species involves the effectiveness of climatic features throughout many years, and a knowledge of these features for any single year is of but little value in the present connection. This consideration involves still another sort of climatic integration that has not yet been mentioned here; namely, the averaging of the effective conditions for long periods of time. This operation has been implied, however, in the preceding treatment of the average length

<sup>24</sup> DAY, P. C., Frost data of the United States, etc. U.S. Dept. Agric., Weather Bureau, Bull. V. 1911.

<sup>25</sup> Summary of the climatological data of the United States, by sections. U.S. Dept. Agric., Weather Bureau. No date. These pamphlets appear to have been prepared about 1909-1910. The data generally extend through 1908 or 1909.



of the frostless season. For the intensity factor of temperature effectiveness it is necessary to employ as data, not the temperature of any single instant, nor the mean temperature of any single day, but what has been termed the *normal mean* temperature for each day of the frostless season. Fortunately, these data have been calculated by BIGELOW and have been made available through publication by the U.S. Weather Bureau.<sup>26</sup> These have been here employed.

The plan of this study is: (1) to sum the normal daily mean temperatures of each station considered, for the period of the average frostless season; (2) to sum the temperature efficiencies corresponding, respectively, to the normal daily means and to the adopted coefficient for  $10^{\circ}$  of variation; (3) to plot both sets of temperature indices so obtained in the form of charts; and (4) to compare the form and location of the climatic areas or zones thus exhibited.

### The temperature indices

As in the case of direct temperature summations, so in that of the summation of temperature efficiencies, it is necessary to establish a temperature which may be taken as a starting-point. This should approximate the temperature at which general plant growth is evident and should be chosen according to the same criteria as are employed by phenology in similar cases. For both series of summations we have taken the rate of growth and development as unity with a daily mean temperature of  $40^{\circ}$  F. ( $4.4^{\circ}$  C.). Normal daily means below  $40^{\circ}$  F. do not occur in BIGELOW's tables. If they did occur, growth on such dates would be taken as nil, on the basis of our assumptions.

For each of the direct summations, the normal daily mean *minus* 39, for the date next following the average date of the last frost in spring, is taken as the first term. To this are added the normal daily means, each decreased by 39, for all dates up to and including the average date of the last frost in autumn. Practically, the summation of the unmodified normal daily means was first made

<sup>26</sup> BIGELOW, F. H., The daily normal temperature and daily normal precipitation of the United States. U.S. Dept. Agric., Weather Bureau, Bull. R. 1908.

for the period and then a quantity equal to 39 times the number of days in the average frostless season was subtracted from the sum.

For the summations of temperature efficiencies, the normal daily efficiencies corresponding, respectively, to the normal daily means of BIGELOW'S tables have simply been added for the same days as in the direct summations, thus giving what may be termed a tentative index of temperature efficiency for growth during the normal frostless season. We shall term this the *efficiency index* and the direct summation will be called the *direct index*. It is these two indices and the charts formed from them that are to be compared.

To obtain the daily temperature efficiencies corresponding to the various normal daily temperature means as the latter are given by BIGELOW, it is necessary merely to deduce them from our basic assumption, namely, that the growth rate is unity at 40° F., and that it doubles for each rise of 10° C. (18° F.) above this. We shall employ the Fahrenheit scale, not because it is in any way as satisfactory as the Centigrade, but because temperature observations in the United States and the published data deduced therefrom have the antiquated form.

If  $t$  be taken as the normal daily mean temperature on the Fahrenheit scale, and if  $u$  be the corresponding temperature efficiency for growth, according to our assumption, then

$$u = 2^{\frac{t-40}{18}}.$$

It is clear that this equation fulfils the assumed conditions, that the efficiency doubles with each rise of 18° F., for, if  $t$  is 40° F., then  $u$  is unity; if  $t$  is 58° F., then  $u$  is 2; if  $t$  is 76° F., then  $u$  is 4; and so on. It becomes necessary, therefore, merely to interpolate between the already known values the various values of  $u$  corresponding to the actual values of  $t$  which are to be dealt with. The equation just given may as well be written

$$\log u = \frac{\log 2}{18} (t - 40),$$

from which the requisite values of  $u$  may readily be obtained. Another way of stating the above relation is this: The tempera-

ture efficiency ( $u$ ) for any Fahrenheit temperature ( $t$ ) is the eighteenth root of 2 effected with an exponent equal to the given temperature *minus* 40. From this the values of  $u$  may be directly calculated. Only one cycle of eighteen quantities, however, needs to be so determined in any case, for the coefficients of the second cycle are double the corresponding ones of the first, etc.

The following table presents the approximate values, derived as above, for the efficiencies corresponding, respectively, to the temperatures (in whole degrees) from 40° to 99° F.

APPROXIMATE EFFICIENCY INDICES FOR TEMPERATURES, IN WHOLE DEGREES, FROM 40° TO 99° F., ASSUMING THE EFFICIENCY TO BE UNITY AT 40° AND TO DOUBLE WITH EACH RISE IN TEMPERATURE OF 18 DEGREES

Temperature, degrees F. ( $t$ )	Efficiency ( $u$ )	Temperature, degrees F. ( $t$ )	Efficiency ( $u$ )	Temperature, degrees F. ( $t$ )	Efficiency ( $u$ )
40.....	1.0000	60.....	2.1603	80.....	4.6662
41.....	1.0393	61.....	2.2451	81.....	4.8490
42.....	1.0802	62.....	2.3331	82.....	5.0396
43.....	1.1226	63.....	2.4245	83.....	5.2384
44.....	1.1666	64.....	2.5198	84.....	5.4424
45.....	1.2123	65.....	2.6192	85.....	5.6568
46.....	1.2599	66.....	2.7212	86.....	5.8782
47.....	1.3096	67.....	2.8284	87.....	6.1090
48.....	1.3606	68.....	2.9391	88.....	6.3496
49.....	1.4142	69.....	3.0545	89.....	6.5972
50.....	1.4696	70.....	3.1748	90.....	6.8566
51.....	1.5273	71.....	3.2986	91.....	7.1258
52.....	1.5874	72.....	3.4283	92.....	7.4048
53.....	1.6493	73.....	3.5629	93.....	7.6960
54.....	1.7142	74.....	3.7024	94.....	8.0000
55.....	1.7815	75.....	3.8480	95.....	8.3144
56.....	1.8512	76.....	4.0000	96.....	8.6412
57.....	1.9240	77.....	4.1572	97.....	8.9804
58.....	2.0000	78.....	4.3206	98.....	9.3324
59.....	2.0786	79.....	4.4902	99.....	9.6980

### Efficiency indices and direct indices for the mean frostless season in the United States

All of the climatological calculations involved in this study have been carried out, and at least once repeated, on a computing machine.<sup>27</sup> The stations employed (179 in number) are those of

<sup>27</sup> The authors wish here to acknowledge with thanks that they have had the assistance, at various points in this work, of Mrs. EDITH B. SHREVE, Mr. H. E. PULLING, and Mr. J. W. SHIVE. It is also a pleasure to state that the study was made possible by the Department of Botanical Research of the Carnegie Institution.

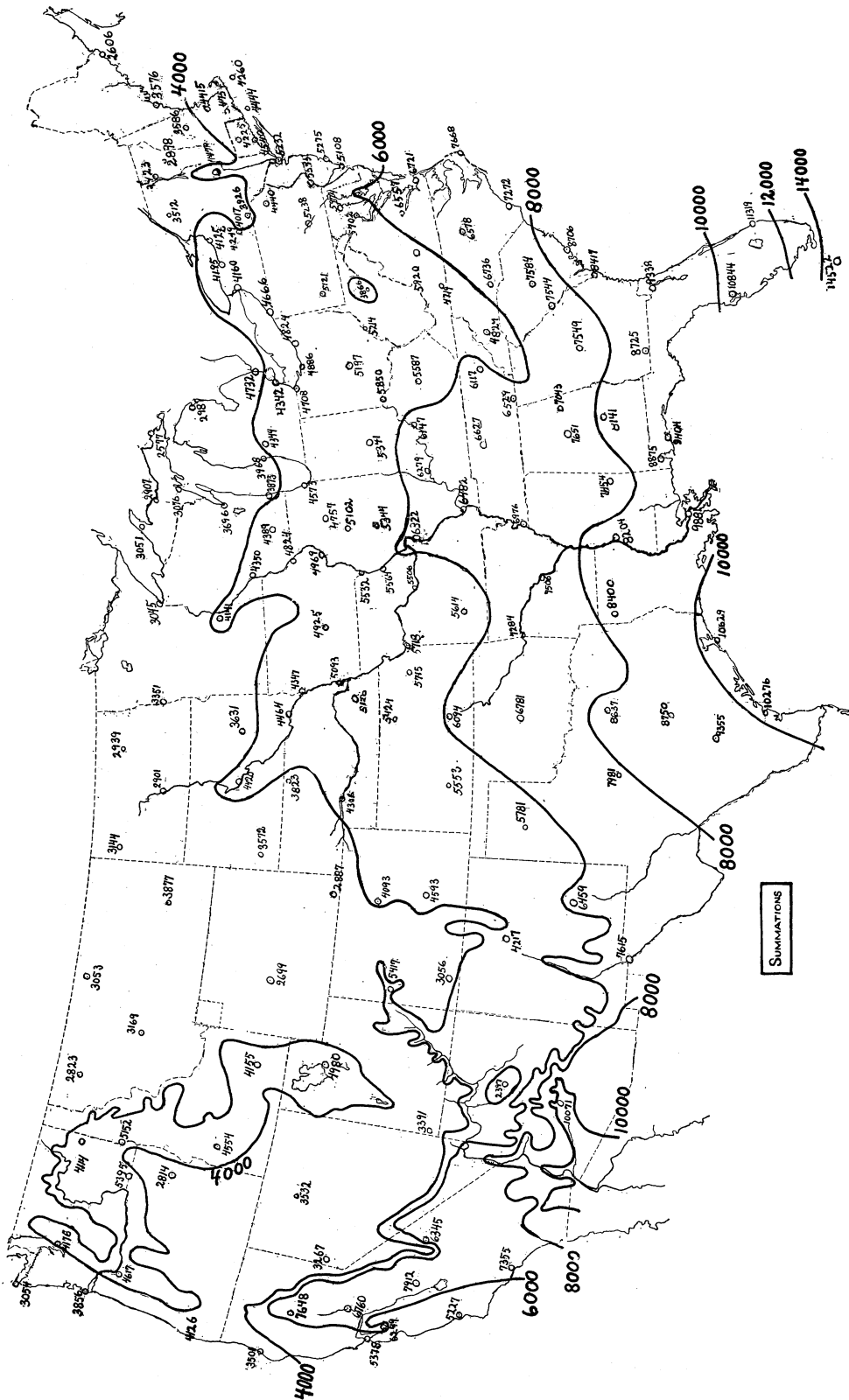
BIGELOW's paper already cited, with a few omissions on account of the lack of corresponding frost data. Each series of summation indices was placed upon a large map of the United States, and the map was then divided into areas by isoclimatic lines, in the usual way. Thus were obtained two charts, one showing the geographic range of the efficiency indices and the other the corresponding range of the direct ones.

It was at once observed that the relations of the different areas to one another are surprisingly similar in the two charts, so that one chart appears about as valuable for bringing out the temperature characteristics of phytogeographic areas as does the other. A detailed study of the two charts, however, made it clear that they differ, as regards the relative form and relative numerical characteristics of their respective zones, in many particulars. The two charts are here presented as figs. 1 and 2. The numerical efficiency data from which these charts were derived (with the aid, at certain points, of probabilities based upon topographic contour lines represented on the original maps<sup>28</sup>) are each placed near the position of the corresponding station, the latter represented by a small circle (for the names of the stations employed, see BIGELOW, *loc. cit.*). To compare the two series of indices, the ratio of each direct index to the corresponding efficiency index was obtained, thus giving a ratio for each station. These ratios have been placed upon a map in a manner quite similar to that used in charting the indices themselves, and the resulting chart, with its isoclimatic lines, is presented as fig. 3.

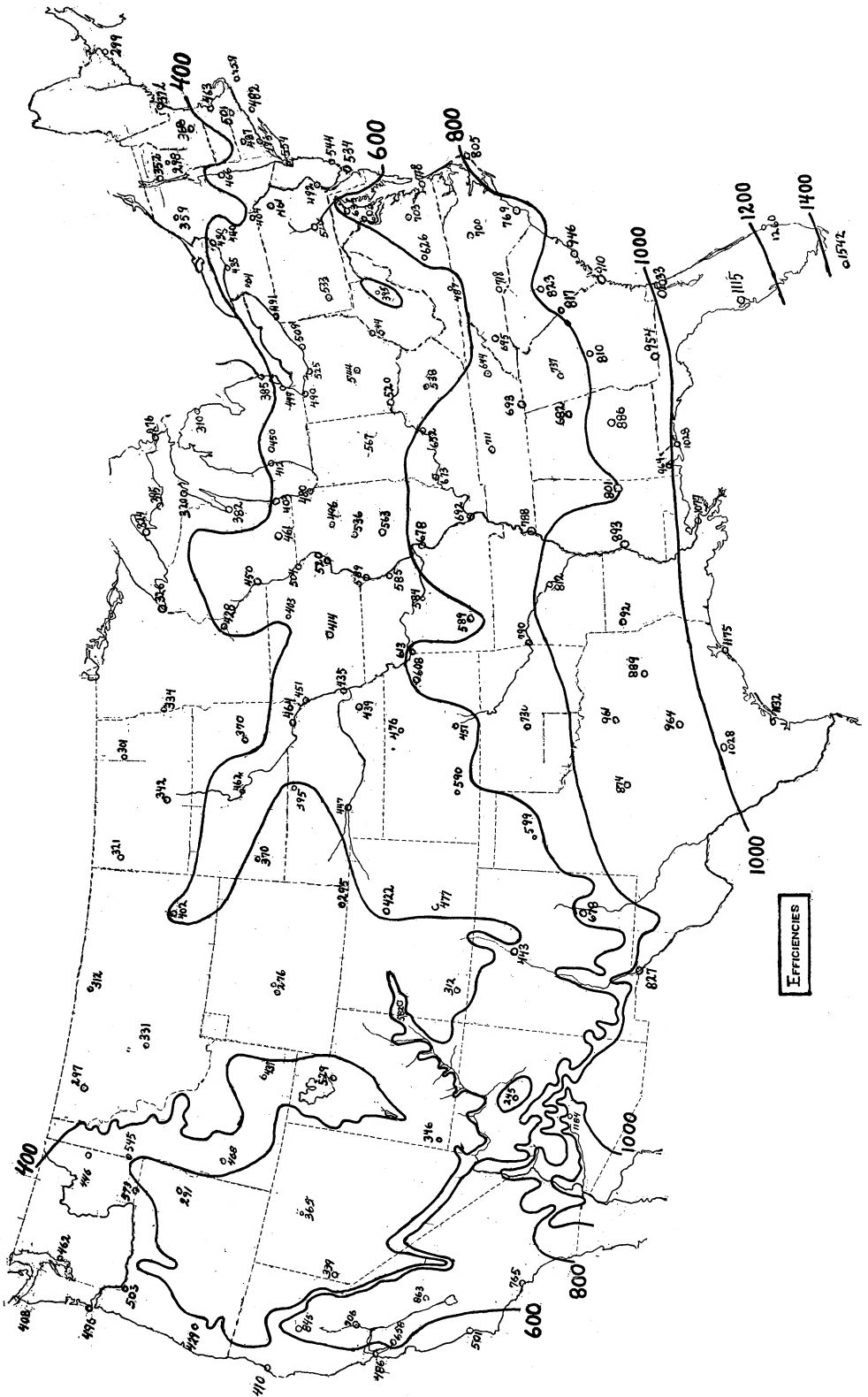
The interpretation of our charts as regards plant distribution will not be taken up here. They are to be studied, of course, in connection with DAY's chart of the average length of the frostless season, with the charts given by B. E. LIVINGSTON, and with any vegetation map of the United States which it is desired to interpret along these lines.

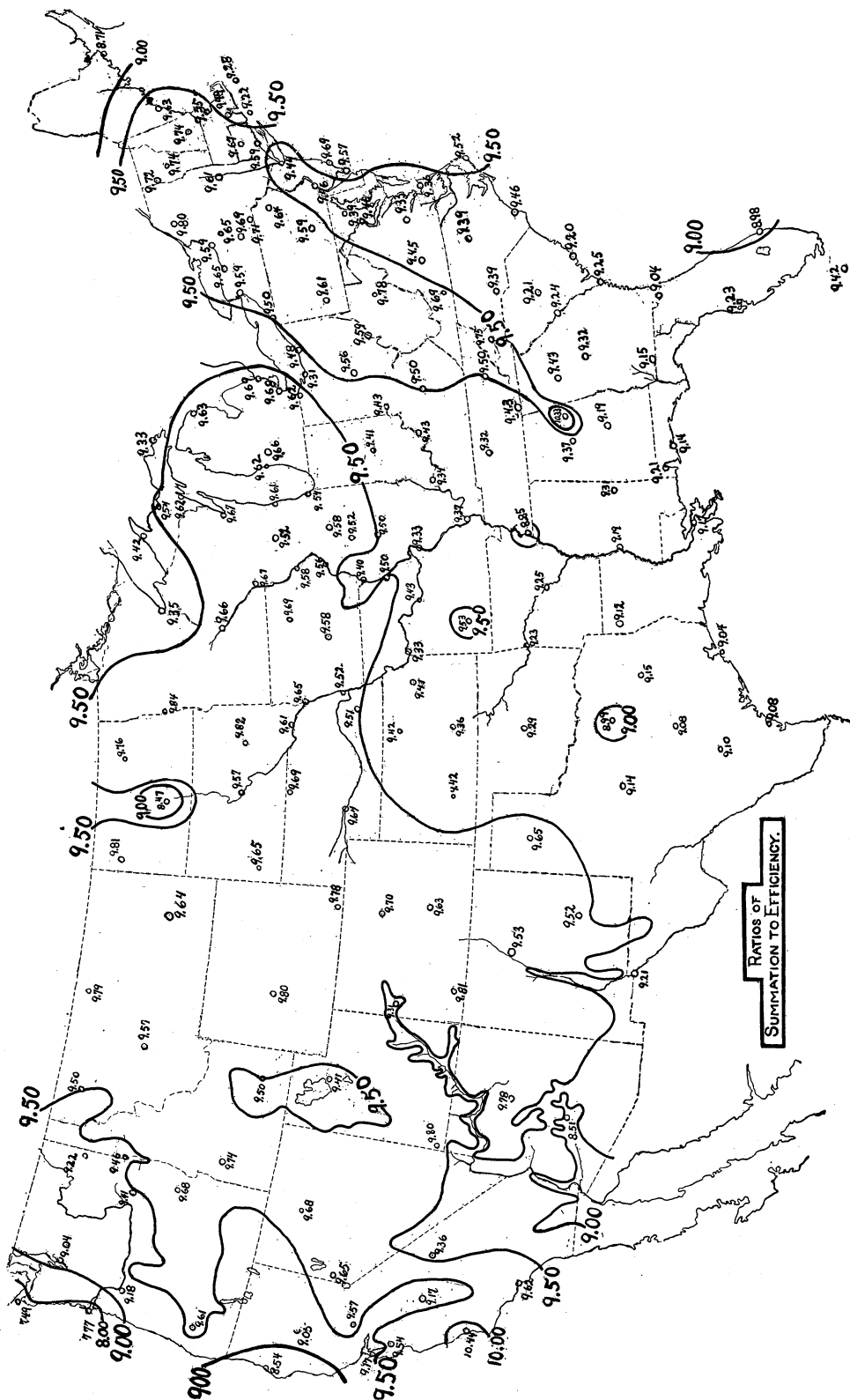
As has been mentioned, the charts of figs. 1 and 2 show a marked similarity in the form and position of the isoclimatic lines which are represented. Of course it is at once to be observed that the direct summation indices are uniformly much larger than the

<sup>28</sup> U.S. Geol. Survey contour map of the United States, 18×28 in.



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corresponding ones of the other series, and simple inspection of the two charts seems to indicate that the former indices are rather uniformly about ten times as great as the latter. No ratio between these two indices really exists which is common to all our stations, but what we wish first to emphasize is that the two charts are outstandingly and even surprisingly alike in the general form of their isoclimatic lines. The stations for which data are available are so irrationally distributed over the country (being relatively closely crowded in the eastern part, with low climatic gradients, and widely separated in the west, with high gradients) that an average ratio, or any other statistical function of the ratio series, must be without meaning, but it is clear from the ratio chart (fig. 3) that ratios between 9.00 and 10.00 characterize almost the entire area of the United States. In other words, for the great majority of stations the magnitude of the ratio in question does not depart more than 5 per cent from the value 9.50. Considering that all our original data must be regarded as only roughly approximate, this appears to indicate a very good agreement between the results of the two methods. We may state, therefore, that *for most of the area of the United States*, the two methods here employed for estimating temperature effectiveness for plant growth give results which agree within the limits of a plus or minus variation no greater than 5 per cent. It will be noted that this statement practically involves the placing of the phenological method of direct summations upon a much more satisfactory basis than this method has heretofore possessed; it now appears that the direct summation method gives the same *general* form of chart as does the other method of temperature integration, and this empirical treatment really ascribes to the former method some degree of the theoretical foundation upon which the latter rests.

The similarity between our two summation charts, however, is only approximate and superficial. If it held rigidly, either of the two charts would suffice for both, and any efficiency index might be deduced from the corresponding direct index, merely by dividing the latter by the proper constant. The efficiency indices are not uniformly ten times the summation indices, nor is there any ratio other than ten which may be assumed with the aim of attaining



greater uniformity of detail in the two charts. The numerical data indicate, furthermore, that it would be quite impossible to make one chart more like the other by choosing other values through which to pass the isoclimatic lines.

The most striking difference between these charts (figs. 1 and 2) is seen in the basin and Pacific regions. Nowhere on the Pacific coast does the efficiency index fall below 400, while the northern half of this coast characteristically exhibits direct indices below 4000, Tatoosh Island, Washington, having a direct index as low as 3054. Thus it has been impossible to draw the lines on the chart of direct summations so as to bring the northern area with indices above 4000 (from Great Salt Lake to the Columbia River) into conjunction with the southern area having the same sort of indices (California, Arizona, etc.). On the efficiency chart these two areas become joined, however. Other less striking quantitative differences are clearly enough indicated, and this sort of inspection establishes the fact that the ratio of the direct summation index to that of efficiency can by no means be regarded as constant for the whole country. It is of course to be remembered that the hypsometric map has been called into requisition in the placing of our isoclimatic lines, the stations for which data are available being far too few and too far apart to give the detailed information which such charts require. Nevertheless, it seems perfectly clear that while the isoclimatic lines may really have other positions than the ones here assigned them (it is safe to suppose that almost every centimeter of these lines would be displaced to some extent if more data were at hand), yet the discrepancies between the two charts are not primarily to be related either to lack of data or to careless or inefficient interpretation of the information at hand.

Our arithmetical treatment of this question of the value of the ratio of the direct index to the index of efficiency brings out the fact that this ratio varies, for the stations employed, from 7.49 (Tatoosh Island, Washington) to 10.44 (San Luis Obispo, California) or 10.33 (Anniston, Alabama). As has been mentioned, the values of these ratios are presented in fig. 3, where lines are shown for the ratio values 8.00, 9.00, 9.50, and 10.00. This chart brings out the geographic distribution of these various values.

What may be the meaning of this new kind of climatic chart, as regards vegetational distribution, plant activity, or any other phenomena influenced by climatic conditions, cannot yet be surmised, but the chart does indicate a very important truth as far as climatology and climatological methods are concerned. If we look upon the normal daily mean temperature as in some way involving a criterion for the approximate evaluation of the naturally effective heat supply, it is shown that the summation of these normals for the period of the frostless season does not give, excepting in a very superficial way, the same chart for the United States as does the corresponding summation of temperature efficiencies following the assumptions here made.

It may be said that the direct index is a measure of one dimension of the temperature factor of a climate, while the efficiency index as here employed measures another dimension. Which of the two dimensions more nearly approximates the measure of the temperature effectiveness of a climate, as far as plant growth is concerned, will no doubt remain for a long time undetermined. The present independent status of the direct summation method for the treatment of temperature data rests upon phenological observations in the open, while the status of the other method of treatment (employing temperature efficiencies instead of the daily mean temperatures themselves) is founded upon deductions from the chemical velocity coefficient of VAN'T HOFF and ARRHENIUS, upon physiological experimentation under more or less controlled conditions, and upon the fact that all physiological processes are chemical in their nature or else depend upon other processes which are chemical. It must be admitted, on physiological grounds, that some sort of efficiency summation seems likely to prove more truthful and more valuable in vegetational-climatic studies than the direct summation of temperatures. The latter method of treatment has no a priori or logical basis (although, as has been seen, it is not altogether without pragmatic or empirical points in its favor), and appears, superficially at least, to be quite arbitrary in its theoretical conception.

The details of the distribution of our various ratio values deserve attention, for they bring out quite unequivocally, not only that

these values do indeed vary, but also that their variations are in accordance with the geographical positions of the stations concerned. It is clear from fig. 3 that the portions of the United States characterized by ratios below 9.00 lie mainly near the margins of the country. The lowest ratios of our series occur in western Washington. Other areas with ratio values below 9.00 are indicated for northwestern California, southeastern California and southwestern Arizona, southeastern Florida, northeastern Maine, and north-central North Dakota. It thus appears that a line representing a ratio of 9.00 may be passed, according to the indications of fig. 3, around the area of the United States, entering within its boundaries only sufficiently to include the areas just mentioned.

On the original chart, from which fig. 3 is taken, were drawn lines representing the ratio values by tenths, from 9.0 to 10.0. From this chart (as of course also from the numerical data given in fig. 3) it is evident that the ratio values with which we are dealing are consistently distributed, with few or no exceptions. An area of high ratios occurs in the Appalachian Mountains, having the highest value at Anniston, Alabama (10.33). Another similar area occupies the Rocky Mountains and appears to extend northward to the Canadian boundary, with maximum values of 9.81 (Williston, North Dakota and Durango, Colorado). A small area of high values lies about Moorehead, Minnesota (9.84), and Huron, South Dakota (9.82). A less pronounced but strongly and consistently indicated area occupies the southern peninsula of Michigan and eastern Wisconsin, the maximum here being at Port Huron, Michigan (9.69). Finally, a somewhat questionably indicated area of high ratio values centers about San Luis Obispo, California (10.44). Interior areas of low ratios require no discussion; they are few, and are generally based upon the evidence of single stations.

From the study of this chart it seems clear that the ratios of direct temperature summations, for the normal frostless season, to the corresponding efficiency summations as here derived, must be considered as a measure of some climatic characteristic. Just what this characteristic may depend upon we are not here attempt-

ing to find out; it obviously has to do with the order of magnitude of the normal daily mean temperatures and also with the distribution of these magnitudes throughout the mean frostless season. There seems little doubt that a mathematical treatment involving limits may bring out the nature of those characteristics of the frostless season which are measured by the ratio as employed in this paper.

### Conclusions

1. The method of direct temperature summations has proved itself to give, *in a broadly general way and for most of the area of the United States*, nearly the same climatic zones as does our method of efficiency summations; for practical purposes and for the present, the former method, till now based solely on phenological observations, seems thus to be placed in closer logical connection with the temperature coefficients of chemical, physical, and physiological processes than has heretofore been the case.

2. The similarity between the results derived by these two methods of temperature integration, however, is only superficial and roughly approximate. The ratios of direct summation to efficiency summation range in magnitude, for the mean frostless season in the United States, from a minimum of 7.49 to a maximum of 10.44.

3. A rational and consistent climatic chart represents the geographical distribution of these ratio values; on such a chart the marginal regions of the country are frequently characterized by low ratios and the two main mountain systems appear to control areas of high values.

4. There seems to be no doubt that the ratio here brought forward quantitatively represents a climatic dimension or characteristic, which appears to be some sort of function of the daily normal temperatures upon which this whole study has been based and of the time distribution of these temperature data within the period of the mean frostless season.